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13. ABSTRACT (Maximum 200 words) This project employs psychophysical techniques to examine the limitations on spatial vision imposed by the first stages in the visual pathway. The appearance of very high frequency interference fringes is distorted, or aliased, by the cone mosaic. Such moire patterns allow us to assess the topography of the cone mosaic in the living eye, clarifying the relationship between cone spacing and resolution. Resolution was also measured under conditions in which only the M or L cones could detect the interference fringe. Visual acuity was little different than it was when both cone types detected the grating, showing that resolution is immune to photoreceptor loss under these circumstances. We recently also established that a phenomenon known for 150 years has been misunderstood, and that it is chromatic aliasing caused by spatial sampling by M and L cones. A device has been constructed to provide objective measurements of the off-axis optical quality of the eye and measurements show that optical quality decline surprisingly little across the visual field. In addition, we have taken advantage of an early nonlinearity in the visual system to measure the spatial responses of the earliest stages in retinal processing.			
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FINAL TECHNICAL REPORT for AFOSR 88-0292

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Project Period: Aug 1, 1988 to Jan 31, 1992

PROJECT SUMMARY

This project employs psychophysical techniques to examine the limitations on spatial vision imposed by the first stages in the visual pathway. Many of the experiments in my laboratory capitalize on the use of laser interferometry, which allows sinusoidal gratings to be formed on an observer's retina that are immune to optical blurring. The appearance of very high frequency gratings is distorted, or aliased, by the cone mosaic. Such moire patterns provide the basis for a number of psychophysical techniques to assess the topography of the cone mosaic in the living eye. These measurements, accompanied by measurements of visual acuity for interference fringes clarify the relationship between cone spacing and resolution. Resolution was also measured under conditions in which only the M or L cones could detect the interference fringe. Visual acuity was little different than it was when both cone types detected the grating, showing that resolution is immune to photoreceptor loss under these circumstances. We recently also established that a phenomenon known for 150 years has been misunderstood, and that it is chromatic aliasing caused by spatial sampling by M and L cones. Interferometry also allows measurements of the optical quality of the eye, and new measurements have been obtained. A device has been constructed to provide objective measurements of the off-axis optical quality of the eye and measurements show that optical quality decline surprisingly little across the visual field. In addition, we have taken advantage of an early nonlinearity in the visual system to measure the spatial responses of the earliest stages in retinal processing.

RESEARCH OBJECTIVES STATED IN ORIGINAL PROPOSAL

1. A psychophysical technique that employs interference fringes to spatially modulate only one cone type will be used to search for aliasing in the middle and long wavelength cone mosaics separately. The identification of aliases under these conditions may reveal the packing arrangement of these cone types in the human fovea.
2. When viewing interference fringes at spatial frequencies near 60 cycles/deg, some observers report the appearance of "red-green zebra stripes" that are qualitatively similar to the achromatic moire patterns previously reported at higher frequencies (110-120 cycles/deg). Experiments will distinguish between two competing hypotheses for this phenomenon: aliasing by M and L cones or nonlinear distortion.
3. The spacing between sampling elements in the short wavelength mechanism will be measured as a function of eccentricity in the living human eye.

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4. Improved estimates of the resolution of the short, middle, and long wavelength cone mechanisms will be obtained with interference fringe stimuli.
5. The origin of the poor resolution for red-green equiluminant gratings will be clarified.
6. Random dot stereogratings will be used to search for aliasing by an array of disparity-sensitive units across the visual field, to determine the factors that limit spatial resolution for changes in depth.
7. A technique that uses moving random dot patterns will search for aliasing by an array of motion-sensitive units across the visual field, to determine the factors that limit the spatial resolution for changes in motion.

RESEARCH STATUS

(1) Consequences of Spatial Sampling for Motion Perception

Nancy Coletta, Carlo Tiana and I have investigated a motion reversal phenomenon observed with drifting interference fringes that we have linked to cone aliasing. This phenomenon allows the spatial sampling rate of the visual system to be measured in the living eye at large retinal eccentricities. The experimental aspects of this work were completed under a previous grant from AFOSR. In the first year of the grant, we completed theoretical work related to the project, including implementation of a model of the phenomenon on a PIXAR image computer. During the second year we also produced a manuscript on this work which is now published in *Vision Research*. A book chapter on some computational aspects of the problem has also been published.

(2) Resolution of the M and L Cones.

During year one, Orin Packer, Nobu Sekiguchi, Nancy Coletta, and I have used chromatic adaptation in an attempt to isolate either the M or L cone mosaic, with the goal of investigating resolution and aliasing with either cone mosaic alone. We have found, surprisingly, that the most extreme forms of chromatic adaptation we can produce do not alter estimates of visual resolution. This suggests that resolution is equal whether either the L or the M cone mosaic is operating alone, or both mosaics are operating together. This results supports the hypothesis that the M and L cones are randomly assigned in the mosaic, allowing for clumps of cones of the same class which could mediate high acuity. This work was briefly described in a publication by the NRC (Williams, 1990)

(3) Contrast Sensitivity for Isochromatic and Isoluminant Interference Fringes

Nobu Sekiguchi and I designed and constructed a new laser interferometer for generating chromatic interference fringes. Such fringes allow sinusoidal modulation in chromaticity as well as luminance while avoiding blurring by the optics of the eye. Experiments with this device were completed and two papers will be submitted to *JOSA* on this work. A copy of Nobu Sekiguchi's thesis, which describes all the experiments accompanies this report. The main conclusions are as follows:

- (a) The foveal resolution limit for red and green isoluminant gratings is 20-25 c/deg when the eye's optics are bypassed.
- (b) The visual system has equal grating summation properties for isochromatic and isoluminant stimuli in a red-green and an S cone directions in color space for middle and high spatial frequencies in the fovea and just outside it.
- (c) Human observers are more than 10 times less efficient than the ideal observer at detecting spatial modulations in either chromaticity or luminance.
- (d) The post-receptoral visual system modifies the shape of the contrast sensitivity functions differently for isoluminant and isochromatic gratings.
- (e) The difference between the isoluminant and isochromatic contrast sensitivity can be explained by a spatial bandwidth that is 1.8 times greater for isochromatic stimuli.
- (f) The visual system has equal spatial bandwidth for isoluminant stimuli in a red-green and an S cone direction in color space.

(4) The Cause of a Chromatic Moire Effect

During the first year of the grant, Nobu Sekiguchi, Orin Packer, and I discovered a new kind of aliasing phenomenon in the fovea that occurs near the resolution limit. We pursued this

phenomenon with some vigor because it was a candidate for aliasing by the M and L cones. Identifying such a phenomenon could allow the packing arrangement of M and L cones to be determined in the human. We now believe that this effect has another origin, and is produced by cone sampling coupled with an early nonlinearity in the visual system. During year 2, we produced a manuscript on this work which is now published in *Vision Research*.

(5) Identification of Chromatic Aliasing by the M and L Cones.

Perhaps the most exciting accomplishment during year two of the grant was establishing a phenomenon whose origin is almost certainly aliasing by the M and L cones. It turns out that this phenomenon has been known for more than 150 years, but has been attributed to temporal factors (Benham's top) instead of spatial aliasing. Fine achromatic gratings seen under conventional viewing conditions can appear to be covered with coarse red and green splotches, and this is just what one would expect from spatial aliasing by the M and L cones. This work has been published as a book chapter (Williams, et al. 1991).

(6) Interpolation and Trichromatic Spatial Sampling

David Brainard and I have investigated the rules the visual system uses to reconstruct spatial patterns under conditions of inadequate sampling. Specifically, we were interested in whether the fine resolution afforded by the luminance channel can improve the resolution of gratings seen only by S cones. Preliminary evidence suggests that a luminance grating added to an S cone grating that is too high to be resolved by the S cones alone does not improve S cone resolution. However, we found that filling-in of S cone signals across the blue-blind area can be influenced by the pattern of excitation of M and L cones. This result suggests that the interpolation rules used by the visual system combine information across cone classes. This work is in press in *Vision Research*

(7) Measurement of the Effect of Adaptation to Chromatic Fringes on Spatial Localization.

Kyunghee Koh, Melanie Campbell, Peter Lennie and I examined the mechanism by which observers adapt to chromatic fringes, such as those produced by chromatic aberration. One of the issues we are addressing is whether the adaptation effects are restricted to color or actually modify spatial localization as well. The evidence so far suggests that color appearance alone is modified with no effect on spatial localization.

(8) Development of a Model of Chromatic Opponency with Random Connections of Cones to Ganglion Cells. Peter Lennie, Bill Haake, and I have been exploring the rules the visual system uses to create ganglion cell receptive fields. This work has resulted in a chapter (Lennie, Haake, and Williams, 1991).

(9) Measurement of the Off-Axis Optical Quality of the Human Eye.

Raphael Navarro, David Brainard, and I solved a number of technical problems associated with measuring the off-axis optical quality of the human eye. We used a variation of the technique introduced by Campbell and Green for assessing optical quality at the fovea. A paper is in preparation describing the results of these experiments. We have also constructed a double pass device for collecting aerial images of a point source imaged on the retina. We used a cooled CCD array that allows us to collect the entire aerial image in one exposure without the need to scan the retina with a slit. Navarro, Artal, and I have submitted a manuscript to *JOSA* on these experiments, and a second manuscript is planned. We found that, with a 4 mm pupil in monochromatic light, the optical quality of the eye is remarkably

good across the visual field. The main off-axis aberration is off-axis astigmatism.

(10) Experiments on the Locus of an Early Nonlinearity in the Visual System.

Chen Bing, Walt Makous, and I completed experiments showing that a nonlinearity in the visual system responsible for spatial harmonic distortion probably resides in the outer plexiform layer of the retina. We have shown that there is some low spatial frequency attenuation introduced prior to the nonlinearity, excluding cones as the locus for the nonlinearity. On the other hand, the spatial bandwidth of the stage prior to the nonlinearity is consistent with the size of individual cones even in retinal regions where there is considerable convergence of the cones onto bipolar cells. This makes the outer plexiform layer the most probable cite for the nonlinear phenomenon. A manuscript has been submitted to *Vision Research*. Earlier work on this nonlinearity, which established a psychophysical technique to estimate the apertures of cones, was published in *Vision Research* (Macleod, Williams, and Makous, 1992)

PUBLICATIONS

- Sekiguchi, N. and Williams, D.R. (1989) Analyses of the Living Human Cone Mosaic with Laser Interferometry. *Japanese Journal of Optics*, 18, 510-515.
- Williams, D.R. (1990) Seeing in the light and in the dark. *Optics and Photonics News*, 1, 36-37.
- Williams, D.R. (1990) The invisible cone mosaic. In *Advances in Photoreception. Proceedings of a Symposium on Frontiers of Visual Science*, (National Academy Press, Washington, D.C.), pp. 135-148.
- Williams, D.R. (1990) Photoreceptor sampling and aliasing in human vision. In: Moore, D.T. (Ed.), *Tutorials in Optics*, Optical Society of America.
- Coletta, N.J., Williams, D.R., Tiana, C.L.M. (1990) Consequences of spatial sampling for human motion perception. *Vision Res.*, 30, 1631-1648.
- Sekiguchi, N., Williams, D.R., and Packer, O. (1991) Nonlinear distortion of gratings at the foveal resolution limit. *Vision Res.*, 31, 815-831.
- Tiana, C.L.M., Williams, D.R., Coletta, N.J., and Haake, P.W. (1991) A model of aliasing in extrafoveal human vision. In: Landy, M., and Movshon, A. (Eds.) *Computational Models of Visual Processing*. MIT Press. pp. 36-56.
- Lennie, P., Haake, W., and Williams, D.R. (1991) The design of chromatically opponent receptive fields. In: Landy, M., and Movshon, A. (Eds.), *Computational Models of Visual Processing*. MIT Press. pp. 71-82.
- Williams, D.R., Sekiguchi, N., Haake, W., Brainard, D., & Packer, O. (1991) The cost of trichromacy for spatial vision. In: Lee, B. and Valberg, A (Eds.) *From Pigments to Perception*. New York: Plenum Press. pp. 11-22.
- Williams, D. (1991) Progress in vision research. *Optics & Photonics News*, 2, 8-9.
- MacLeod, D.I.A., Williams, D.R. and Makous, W. (1992) A visual nonlinearity fed by single cones. *Vision Res.*, 32, 347-363.
- Galvin, S.J. and Williams, D.R. No aliasing at edges in normal viewing. *Vision Res.* (submitted).
- Brainard, D.H., Williams, D.R. Spatial reconstruction of signals from short-wavelength cones. *Vision Res.* (submitted).
- Chen, B., Makous, W. and Williams, D.R. Serial spatial filters in vision. (submitted).
- Packer, O. and Williams, D.R. Blurring by fixational eye movements. *Vision Res.* (submitted).

Williams, D.R., Sekiguchi, N., Brainard, D., Haake, P., and Packer, O. (in preparation) Spatial aliasing by red-green chromatic mechanisms. To be submitted to *Nature*

Packer, O., and Williams, D.R. (in preparation) Eye movements and visual resolution. To be submitted to *Vision Res.*

Makous, W., Williams, D.R., MacLeod, D.I.A. (in preparation) A nonlinearity in early vision. To be submitted to *J. Opt. Soc. Am.*

Chen, B., Makous, W., and Williams, D.R. (in preparation) Locus of an early nonlinearity in the visual system. To be submitted to *J. Opt. Soc. Am.*

PERSONNEL ENGAGED ON PROJECT

The following personnel have been actively involved in the projects described above:

Pablo Artal. Visiting Scholar from Instituto des Opticas, Madrid, Spain.

David Brainard. Postdoctoral fellow supported by AFOSR and NRSA fellowship.

Melanie Campbell. Visiting Scholar from the University of Waterloo.

Bing Chen. Postdoctoral Fellow, supported in part by AFOSR.

Nancy Coletta. Former postdoc, now an assistant professor at the University of Houston.

Susan Galvin. Graduate student supported by University fellowship.

Bill Haake. Systems Analyst supported by AFOSR.

Kyunghee Koh. Postdoctoral fellow supported 50% by AFOSR.

Peter Lennie. Faculty Member.

Walter Makous. Faculty Member.

Rafael Navarro. Visiting scholar from Instituto des Opticas, Madrid, Spain.

Orin Packer. Postdoctoral fellow supported by NRSA Fellowship.

Al Russell. Electronics engineer supported by AFOSR.

Nobutoshi Sekiguchi. Graduate student supported by Olympus Optical Corporation.

Carlo Tiana. Graduate student supported by AFOSR.

LIST OF INTERACTIONS

Presentations at Professional Meetings:

Chen, B., Makous, W. and Williams, D.R. A nonlinearity localized in the outer plexiform layer. Association for Research in Vision and Ophthalmology, Sarasota, FL, 1989.

Packer, O., Williams, D.R., Sekiguchi, N., Coletta, N.J. and Galvin, S. Effect of chromatic adaptation on foveal acuity and aliasing. Association for Research in Vision and Ophthalmology, Sarasota, FL, 1989.

Lennie, P., Haake, P.W. and Williams, D.R. Chromatic opponency through random connections to cones. Association for Research in Vision and Ophthalmology, Sarasota, FL, 1989.

Lennie, P. Haake, P.W. and Williams, D.R. Chromatic opponency through indiscriminate connections to cones. Optical Society of America, Orlando, Fla., October, 1989.

Williams, D., Coletta, N., Tiana, C., Haake, W. Spatial sampling & image motion, Workshop on Computational Models of Visual Processing, Cold Spring Harbor, June 1989.

Williams, D.R. Photoreceptor sampling of moving images. Applied Vision Topical Meeting, San Francisco, CA, July 1989.

Williams, D.R., Coletta, N., Tiana, C. and Packer, O. Spatial sampling, image motion, and visual resolution. "Optics, Physiology and Vision," The Westheimer Symposium, San Francisco, CA, August 1989

Lennie, P. Haake, P.W. and Williams, D.R. Chromatic opponency through indiscriminate connections to cones. Optical Society of America, Orlando, Fla., October, 1989.

Packer, O. and Williams, D.R. Eye movements and visual resolution. Association for Research in Vision and Ophthalmology, Sarasota, FL, 1990.

Koh, K., Lennie, P., and Williams, D.R. Mechanisms of adaptation to chromatic fringes. Association for Research in Vision and Ophthalmology, Sarasota, FL, 1990.

Williams, D.R., Sekiguchi, N, and Packer O. Spatial aliasing by chromatic mechanisms. Association for Research in Vision and Ophthalmology, Sarasota, FL, 1990.

Sekiguchi, N., Packer, O. and Williams, D.R. Spatial sampling by chromatic mechanisms in human vision. Society for Photographic Science and Engineering, Rochester, NY, 1990.

Packer, O. and Williams, D.R. Do eye movements affect visual resolution? Society for Photographic Science and Engineering, Rochester, NY, 1990.

Williams, D.R., Sekiguchi, N. and Packer, O. Spatial sampling by the human foveal cone mosaic and its implications for color vision. International Congress of Eye Research, Helsinki, Finland, 1990.

Williams, D.R. Interpolation and trichromatic spatial sampling in foveal vision. *Advances in Understanding Visual Processes*. Roros, Norway, 1990.

Sekiguchi, N, Williams, D.R. and Brainard, D.H. Foveal resolution limit for chromatic interference fringes. *Optical Society of America annual meeting*, San Jose, California, November 3-8, 1991.

Williams, D. Spatial sampling in human vision. *Curso Interuniversitario para Postgraduados Sobre meeting*, Madrid, Spain, November 25-27, 1991.

Williams, D. The cost of trichromacy for human vision. *Curso Interuniversitario para Postgraduados Sobre*, Madrid, Spain, November 25-27, 1991.

Navarro, R, Artal, P. and Williams, D.R. Optical quality of the human eye across the visual field. *Ophthalmic and Visual Optics*, OSA meeting, Santa Fe, New Mexico, January 28-30, 1992.

Williams, D.R. The mechanisms that prevent aliasing in the visual system. *Ophthalmic and Visual Optics*, OSA meeting, Santa Fe, New Mexico, January 28-30, 1992.

Williams, D.R. Perceptual consequences of the trichromatic cone mosaic. *Advances in Color Vision*, OSA meeting, Irvine, California, January 31-February 1, 1992.

Sekiguchi, N., Williams, D.R. and Brainard, D.H. Contrast sensitivity for isoluminant and isochromatic interference fringes. *Advances in Color Vision*, OSA meeting, Irvine, California, January 31-February 1, 1992.

Brainard, D.H. and Williams, D.R. Spatial reconstruction of signals from short-wavelength cones. *Advances in Color Vision*, OSA meeting, Irvine, California, January 31-February 1, 1992.

Colloquia:

Color vision and the cone mosaic, New York University, 1988.

Limits of spatial vision, University of Alabama, 1988.

A nonlinearity in early spatial vision, Columbia University, 1989

Aliasing in human foveal vision, Columbia University, 1989

Spatial sampling in human vision, University of Texas, Austin, 1989

Image motion and spatial sampling, University of California, San Diego, 1989

On measuring the cone mosaic in the living human eye. *Eye Research Institute*, Boston, MA, 1989

There is more to seeing than meets the eye. University Forum, University of Rochester, 1989.

Spatial sampling in human vision. University of Waterloo, Waterloo, Canada, 1990.

Spatial aliasing by chromatic mechanisms in human vision, Polaroid Corporation, Boston, MA, 1990.

Spatial aliasing by chromatic mechanisms in human vision, University of Michigan, Ann Arbor, MI, 1990.

The cost of trichromacy for spatial vision, Laboratoire de Physique Appliquee du Museum, Paris, France, 1990.

The cost of trichromacy for spatial vision, University of Valencia, Valencia, Spain, 1990.

The cost of trichromacy for spatial vision, C.S.I.C. Instituto de Optica, Madrid, Spain, 1990.

The cost of trichromacy for spatial vision, Rochester Institute of Technology, Rochester, New York, 1991

Consulting:

Visited the Night Vision and Electro-Optics Laboratory, Fort Belvoir, MD. to discuss potential improvements in night vision goggles worn by Army helicopter pilots, 1990.

Inventions/Patents:

None